GROWTH KINETICS AND LONGEVITY OF THE SALT MARSH RUSH *JUNCUS ROEMERIANUS*

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ABSTRACT   Vegetative development of shoots of the tidal marsh rush *Juncus roemerianus* was studied quantitatively in short (S), medium (M), and tall-leaved (T) populations. Shoot longevity varied between populations, with some shoots producing one leaf and living 4 months, while others produced seven leaves and lived over 4 years. An equation was developed from plastochron and leaf-age determinations to estimate shoot age in each population studied. Major morphological events common to all populations were (1) cessation of growth of the first leaf produced on an erect stem when growth of the second leaf was initiated, and (2) death of the leaf from the tip downward. Although the time period was variable, growth rates of leaves equalled their death rates in each population during maximum periods of growth and subsequent decline. While growth and death rates were similar between two of the populations (M, T) investigated, these rates were vastly different from those representative of the third population (S). Growth and death kinetics for leaves on individual shoots involved cyclic phenomena represented by a series of greatly overlapping harmonic curves. Each shoot reached a maximum carrying capacity expressed as linear biomass. Although living portions were often distributed over three or four leaves, the total equated to two mature living leaves for the medium (M) and tall-leaved (T) populations. In the short-leaved population (S), the maximum amount of biomass attained by a single shoot during its life span equalled that of one mature leaf. A peculiar steady-state or homeostasis in growth and net productivity exists in each population. Short-lived shoots in the short-leaved population (S) was shown to have a rapid turnover of replacement rate, which is responsible for a high net productivity equal to or exceeding the net productivity of both the medium and tall-leaved populations. Although the cause of variation in basic growth patterns between the three populations was not investigated, both genetic and environmental factors may be involved.

INTRODUCTION

Tidal marshes are composed primarily of a herbaceous flora, the major constituents of which possess rhizomes. Through vigorous rhizome growth some of these herbaceous species dominate vast areas of tidal marsh. Black rush or needle rush, *Juncus roemerianus* Scheele, is a major constituent of tidal marshes located in estuaries on the South Atlantic and Gulf coasts of the United States (Eleuterius 1976a). Correspondingly, the species contributes to the energetics of many estuaries. Knowledge of shoot development, rates of leaf growth, and longevity of shoots is essential and basic to our understanding and assessment of net primary productivity, standing crop, and turnover of tidal marsh angiosperms. Estimates of growth, expressed as or based on standing crop, serve as a general index of comparison, but fail to reveal the details or kinetics of growth. Vegetative growth patterns of the major kinds of herbaceous plants are very different, although this fact has not been elaborated upon previously. Furthermore, there often appears to be considerable variation in growth rate, net primary productivity, and turnover between separated populations of the same species.

Steward (1968), Richards (1969), Dormer (1972), and Williams (1975) present excellent reviews of methodology and discussions on the quantitative analysis of plant growth, whereas Pratt (1941), Williams (1964), Williams and Rijven (1965), Koller and Kigel (1972), and Evans (1972) used

successive linear measurements extensively to record and analyze plant growth.

The present work arose from previous studies to develop criteria for evaluating tidal marshes. We found that in some populations of *J. roemerianus* from 1 to 8 leaves were produced sequentially in a synchronized system from the erect stems and that these shoots bearing different numbers of leaves lived different lengths of time. In the present study, our objectives were to provide a reliable method of studying the developmental pattern of the shoot; to determine the morphological pattern of the shoot over a long period of time; to compare the growth rates of leaves, shoot longevity, and leaf death rates of representative plants in populations of *J. roemerianus* with very short, medium, and tall leaves (stand height); and to use the resulting data in estimating shoot age and turnover.

The three populations selected for study span the major structural characteristics of most populations of *J. roemerianus* in the coastal region bordering the northern Gulf of Mexico. These populations are located in tidal marshes at Belle Fontaine Beach (BFB), Grand Bayou (GB), and Salt Flats (SF) in the coastal area of Jackson County, Mississippi. Hereafter in this paper the above codes are used in reference to the location of the respective rush populations. The plants with shortest leaves but greatest density of shoots (N/m^2) are found in the SF population inhabiting areas with very sandy surface soil underlaid with clay at 2 to 4 feet. Rushes with leaves of medium length and density of shoots intermediate to those found at SF and BFB are found at GB. The soil at GB is a sandy clay. At BFB the

soils are highly organic, composed primarily of peat, and
the plants have the longest leaves and lowest density of
shoots. The soil water of the SF population is hypersaline
(60 to 300 ppt). Soil water from the tidal marshes around
GB is generally moderate-to-low in salinity (5 to 20 ppt)
while that in the BFB marshes is relatively low (0 to 6 ppt)
(Eleuterius 1974).

METHOD

Twenty young shoots, each bearing a first leaf less than
20 cm in length, were selected at random in each of the
three plant populations. The shoots were marked with plastic
rings and numbered during November 1976. Initiation of
new leaves on each shoot was noted; the length of each
live leaf and the length of the dead segment of older leaves
were measured monthly for 28 months. A storm washed
away our markers forcing us to conclude the study. Lon-
gevity of individual shoots and their respective growth
curves (leaf length plotted against time) were determined
from the obtained data and were compared to other shoots
within and between populations.

RESULTS

Shoot Development

Sympodial branching characterizes the vegetative growth
of mature plants of *J. roemerianus* (Eleuterius 1976b). As
the rhizome apex turns upward, division of the apical
meristem formed a rhizome apex (continuation bud) simul-
taneously with the production of an erect shoot. This growth
phenomenon is also common to other angiosperms (Bennett-
Clark and Ball 1951, Holttum 1955). Thus, the youngest
shoot, bearing one leaf, is always proximal to the rhizome
apex of an interconnected series of rhizomes and shoots,
and the oldest shoot, often with three or more leaves, is
the most distal to the apex (Figure 1A). The number of
mature leaves produced on an individual shoot, along with
other data to be given later, can be used to estimate the age
of that shoot (Figure 1B) within a given population with
relative precision. Young leaves of an individual shoot arise
from short stems and grow through a slit in the base of
the preceeding leaf in an alternating or distichous manner
(Figure 1C).

Leaf Production and the Plastochron

The number of leaves produced on each erect stem was
variable within and between the three populations (Table 1).
About half of the shoots produced only one leaf in the SF
and BFB populations. Erickson and Michelini (1957) des-
cribed the plastochron as the time interval between two
similar developmental events on the same shoot. Here the
plastochron of *J. roemerianus* was variable and equal to the
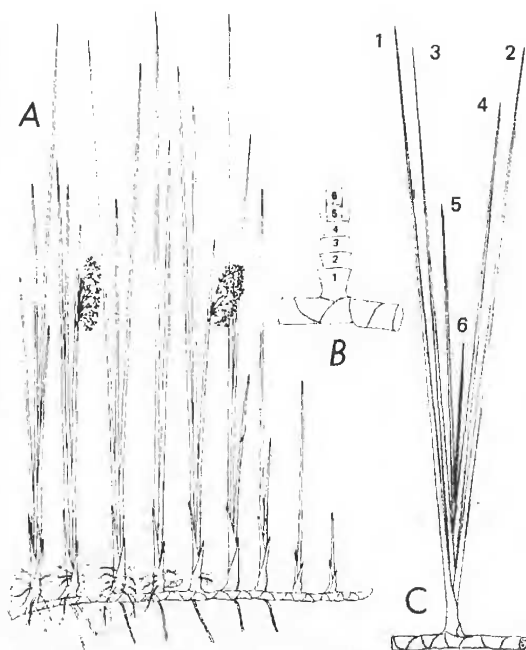time required to produce one mature leaf.

Figure 1. Morphological characteristics of *Juncus roemerianus*. An
interconnected series of rhizomes and shoots are shown in A.
Younger shoots with fewer leaves are found near the rhizome apex,
older ones farther away. B. Diagram of short erect stem connected
to rhizome segment. Numbered, close-set nodes indicate origin of
sequentially produced leaves on each erect shoot. C. The distichous
or alternating arrangement of leaves on single shoot. Numbers corres-
pond to sequence of leaf production.

TABLE 1.

Distribution of leaves on shoots of *Juncus roemerianus* in three
different populations. Shoots are ranked according to total
and average number of leaves produced on each shoot
selected for study. Number of leaves indicates total
or maximum number attained prior to shoot
death or termination of the study.

Population	Number of Leaves per Shoot					
	1	2	3	4	5	X̄
Salt Flats (SF)	10	9	1			1.6
Grand Bayou (GM)	7	5	4	4*		2.3
Belle Fontaine Beach (BFB)	9	4	2	4*	1**	2.2

*One or more of these shoots may have produced a fifth leaf.
**This shoot may have produced a sixth leaf.

All second leaves were produced during the spring at SF,
while in the GB and BFB populations, most second and third
leaves were produced during the summer and following spring
(1978), respectively (Figure 2). Although the seasonality

of secondary leaf production on individual shoots was similar for both GB and BFB, some shoots at BFB exhibited a precocious leaf development indicative of accelerated growth in very early spring.
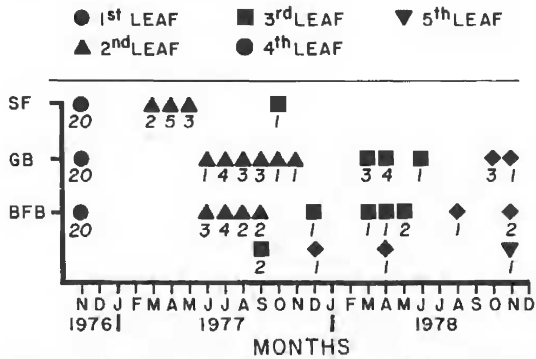

Figure 2. Populational differences in leaf production. Symbols indicate chronological order and array of leaf production on individual shoots. Subscripted numbers indicate number of shoots producing a second, third, fourth, or fifth leaf during a particular month.

Leaf Length

The range and average of the maximum heights (lengths) attained by mature leaves of *J. roemerianus* were distinctly different between the three populations as shown graphically in Figure 3. Leaves at BFB ranged from about 110 to 170 cm, and averaged 142 cm in length, and at GB from 65 to 133 cm, with an average of 104 cm. The population at SF had the shortest leaves, ranging from 11 to 64 cm and averaging 26 cm.

Leaf Growth and Death Curves

Representative growth and corresponding death curves for leaves produced on single shoots from three populations are shown in Figure 4. These size-versus-time plots show the cumulative increase in height (length) of successive leaves on three individual shoots, each of which represents a different population. The kinetics of shoot growth as shown in the BFB and GB curves are very similar (Figure 4: BFB, GB). Both illustrate several overlapping, yet, typical sigmoid curves with characteristic logarithmic (exponential), linear (grand), and senescent phases (Blackman 1919, Pope 1932). Plots of monthly averages from combined data (all shoots) for each population produced a similar but smoothed and flattened curve in comparison to that of individual shoots. Growth of the first leaf produced on an erect stem ceased when growth of the second leaf was initiated and represented a plastochron (Erickson and Michelini 1957). The process held for all subsequent leaves on an individual shoot and for all shoots producing more than one leaf in all populations.

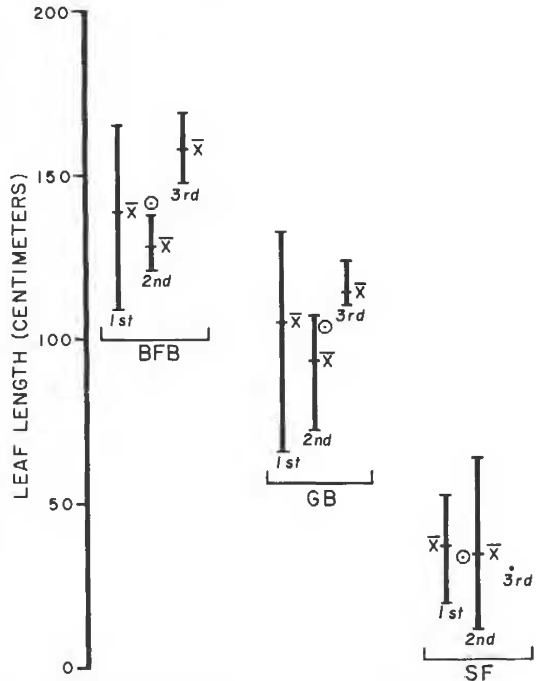As the second leaf matured the first leaf began to die

Figure 3. Populational differences in leaf lengths. Comparative data showing range and average mature leaf lengths for three populations studied. Circled dot ⊙ indicates average leaf length based on array of first, second, and third leaves produced in each population.

from the tip downward. This same relationship held between the third and second leaf and so on. Very little increase in leaf length occurred during winter months, whereas rapid growth characterized the late spring, summer, and early fall. Note the flattened curve for January and February in Figure 4. Although the reason for this is unclear, second leaves were generally slightly shorter than first or third leaves (see Figure 3). Growth of the third leaf began several months before the first and second were completely dead.

No consistent pattern was obtained for the curve representing senescence. The senescence phase of the growth curve often equalled the slope of the curve during the exponential phase, but senescence generally occurred very rapidly, represented by a graphically sharp decline. Death of leaf tissue represented by this steep decline in the senescent curve was not, however, restricted to any particular period of time and we could not assign any probable cause to it. Furthermore, there was a maximum amount of living leaf tissue sustainable on a single shoot and, although the living segments may have been distributed between two, three, or four leaves, the amount was not apparently greater than that of two entire living leaves representative of the mature component of the respective population. This observation held true regardless of the location of the population.

Dead leaves remain standing for several years or more in the BFB population, but are rapidly swept away by tides at SF. Fewer dead-standing leaves were found in the GB population in comparison with those at BFB.

Shoot development at SF is obviously an abbreviated process (Figure 4). Plots of all other SF shoots investigated are similar.
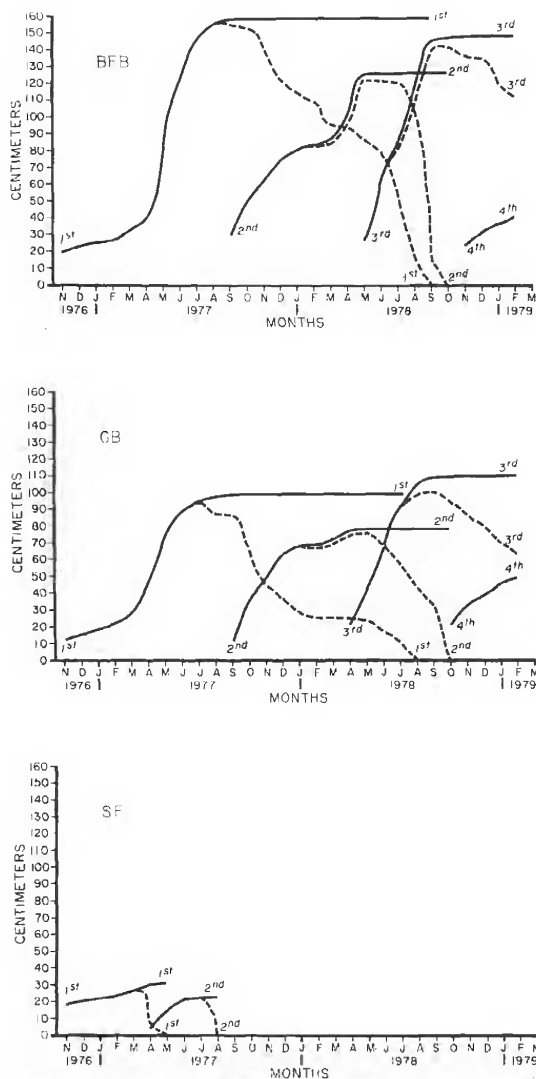

Figure 4. Growth and death curves for leaves produced on a single shoot of *Juncus roemerianus* in three different populations. Solid and dotted lines show size of the living portions of leaves versus time, the accumulative increase in leaf length, the sequential initiation of new leaves, the corresponding cessation of growth and senescence of leaves of representative shoots from each population.

Leaf Growth and Death Rates

Calculation of growth rates also indicated that the period of greatest leaf growth was during spring, summer, and early fall (Table 2). Average growth rates during this study period were very similar in the GB and BFB populations (about 0.7 and 1.0 cm per day, respectively). An average of 0.2 cm per day occurred during the period of maximum growth for the shoots observed in very early spring at SF. Although the growth rate of individual leaves was variable, we surmise that these estimates represent the exponential phase for new cohorts and, thus, are characteristic of the maximum sustainable or annual growth rate in the respective populations. The maximum daily growth of a single leaf in the BFB, GB, and SF populations and the months of occurrence were 1.5 cm (July), 1.1 cm (September), and 0.4 cm (February), respectively.

TABLE 2.

Average growth rate (cm/day) of mature leaves of *Juncus roemerianus* during the months in which maximum growth occurred (shown in parenthesis). Number of leaves used in determining growth rate of successive leaves on individual shoots shown in brackets.

Population	Leaf 1 (Mar, Apr, May)	Leaf 2 (Jul, Aug, Sep)	Leaf 3 (Apr, May, Jun)
Salt Flats (SF)	*0.2 [10]		
Grand Bayou (GB)	0.7 [13]	0.7 [8]	0.8 [4]
Belle Fontaine Beach (BFB)	1.0 [11]	1.0 [5]	1.3 [3]

*(Feb, Mar)

Calculation of death rates of leaves from the apex downward indicated that summer and fall were the periods of greatest leaf death (Table 3 and Figure 4) although some leaves died rapidly during winter. Average death rates during this period were also very similar in the GB and BFB populations (about 0.8 and 1.0 cm per day, respectively). An average of 0.7 cm per day occurred in late spring at SF. During this period death rate briefly exceeded growth rate. The maximum daily rate of death of a single leaf in the BFB, GB, and SF populations, and the months of occurrence were 4.2 cm (July), 2.2 cm (October), and 1.4 cm (May), respectively.

Leaf Longevity

Leaves of shoots in SF, GB, and BFB populations lived an average of 7.5, 16, and 14 months, respectively, based on all leaves on all shoots investigated. However, average age of leaves, based on shoots that produced more than one leaf, was 7, 14, and 12 months for SF, GB, and BFB, respectively

(Table 4). On shoots producing more than one leaf, the first leaf generally lived longer than the second in all populations examined. Third and fourth leaves usually lived as long as, or longer than, the second. Some leaves lived 22 months. Leaf longevity was very similar between the BFB and GB populations but contrasted sharply with that at SF.

TABLE 3.

Average death rate (cm/day) of mature leaves of *Juncus roemerianus* during the months in which maximum death occurred (shown in parenthesis). Number of leaves used in determining death rate of successive leaves on individuals shoots shown in brackets.

Population	Leaf 1 (Sep, Oct, Nov)	Leaf 2 (Jul, Aug, Sep)	Leaf 3 (Aug, Sep, Oct)
Salt Flats (SF)	*0.7 [9]		
Grand Bayou (GB)	0.6 [13]	1.0 [8]	†0.3 [4]
Belle Fontaine Beach (BFB)	0.9 [10]	1.4 [4]	†0.3 [3]

*(May, Jun)

†About one third of leaf was dead when experiment ended.

TABLE 4.

Leaf longevity. Average and maximum of months that leaves of *Juncus roemerianus* live in different populations. Leaves are grouped based on chronological development on individual shoots in each population. Number of leaves used in determinations shown in parenthesis.

Population	Leaf 1 $\overline{X}$ Max	Leaf 2 $\overline{X}$ Max	Leaf 3 $\overline{X}$ Max	Leaf 4 $\overline{X}$ Max	Leaf 5 $\overline{X}$ Max
Salt Flats (SF)	8 17 (15)	7 16 (8)			
Grand Bayou (GB)	15 22 (16)	13 17 (12)	15 16 (16)		
Belle Fontaine Beach (BFB)	15 22 (16)	11 14 (8)	11 15 (16)	12 14 (4)	15 (1)

Shoot Longevity

The number of leaves produced and the life span of each leaf on an individual shoot determine the longevity of that shoot. The shoots of the BFB and GB populations live about twice as long as those in the SF population (Figure 5). Mortality of shoots began 4 months after the study was initiated and continued periodically thereafter. The average shoot life at SF was 11 months with one shoot living 22 months. Average shoot life at GB was 25 months with seven shoots alive at the end of 28 months. Projected longevity, based on average life span and vitality of leaves studied in

the GB population, indicated that some of the shoots studied probably lived about 40 months. Although seven shoots were alive at the end of the study period, no new leaves were produced and those living leaves present were dying.
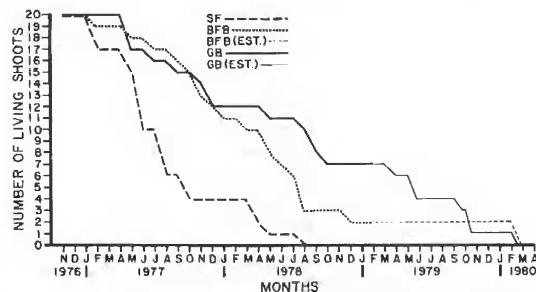

Figure 5. Shoot longevity. The life spans of three cohorts of shoots, each representative of a different population of *Juncus roemerianus*. Each cohort was composed of 20 shoots for a total of 60. Lines indicate mortality and survival of each group over time.

Similarly, the average longevity of shoots at BFB was 21 months with two shoots alive at the end of 28 months. Projected longevity, estimated from average life span and vitality of leaves from this population, indicated that 10% of the shoots may live about 40 months in the BFB population. Production of a sixth or seventh leaf certainly was possible on two of the shoots at BFB because both were very vigorous and new leaves had just been initiated. Moreover, shoots with six and seven leaves, which have been observed in the GB and BFB populations, respectively, clearly indicate that some vegetative shoots of the rush *J. roemerianus* may live 4 years or longer.

DISCUSSION

We found during this study that: (1) frequent linear measurements of leaf length are a valuable and sensitive aid in the interpretation of growth phenomena in *J. roemerianus*, (2) growth curves of an individual rush shoot are actually a complex network of overlapping curves or series of correlations between linear growth and time, (3) considerable variation in the kinetics of growth occurs between populations of *J. roemerianus*, (4) these populational differences appear to be caused by the location and the environmental conditions peculiar to respective populations, although it certainly was possible that they represented genetically distinct ecotypes, (5) our data provided basic information for making numerous types of estimates, such as: biomass, shoot age, leaf age, net productivity, and turnover in populations of *J. roemerianus*.

For emphasis, we found that developmental events of the shoot were repeated with the initiation of each new leaf and that the time intervals between leaves on the same shoot were highly variable. Therefore, the plastochron or time interval determined from the present study is equivalent to

the period required to complete the several developmental stages of one leaf (Erickson and Michelini 1957). Linear measurements of individual leaves and the plastochron age of shoots are nondestructive ways of obtaining data basic to net productivity estimates.

Although shoot development for the three populations examined is similar in the consistent morphological pattern of sequential leaf production and death, and in tracing the classical sigmoid growth curve, shoot characteristics are very different in other ways. These populational differences are summarized as follows: (1) leaf production—the number of leaves produced per shoot, (2) leaf length—the most obvious difference between the three populations, (3) leaf growth rate—equalled by leaf death rate within each population but variable between populations, and (4) leaf and shoot longevity—both lived much longer in the GB and BFB populations than at SF.

The BFB population is composed of plants with long leaves (110 to 170 cm, $\overline{X}$ = 142 cm) which remain standing for a long time after they die. About two thirds of the aerial standing crop are dead leaves. A smaller number of living shoots (about $500/m^2$) occupy the marsh surface at BFB in comparison to those found at GB ($700/m^2$) and SF ($2,000/m^2$) (Eleuterius 1980). The vitality of individual shoots at BFB is very different from one another with a small percentage of shoots in the population possessing great vigor and living several years. This contrasts with shoots in populations at GB and SF, where their growth patterns are most consistent. Furthermore, dead-standing leaves comprise about one fourth of the standing crop at GB in comparison to about one tenth of the vegetation at SF.

The vigor of individual shoots is, as with all tidal marsh plants, ultimately tied to the physical and chemical energetics of the estuary. Dead leaves readily accumulate in populations protected from high wind and wave activity; consequently, growth of living shoots is suppressed, probably because of competition for light. Populations exposed to frequent tidal action, where dead-standing leaves are readily swept away, are more apt to represent a steady state of continuous robust growth. The BFB population is in a protected location and consequently has a high ratio of dead to living leaves. The GB population is more exposed and the SF population is very exposed to wind, wave, and tidal action in comparison to that at BFB. Other environmental factors, such as the concentration of sea salts in the soil solution, obviously affect, to some extent, the growth of *J. roemerianus.*

In all of the populations studied, a reliable indication of the biomass can readily be obtained directly from plotted data. For example, there may be several living leaves on a shoot, but only one leaf increases its length at any living shoot, at any time. Therefore, the living component of leaves, which are not growing, decreases in size (linear measurement) because of leaf death. In the GB and BFB populations, the biomass sustained per shoot is equivalent

to that of two entirely living, mature leaves. However, this living tissue may be distributed over 3 or 4 leaves, depending on the stage of shoot development. The "two living leaves" concept represents the maximum carrying capacity of an individual shoot in these two populations. In each population studied, leaf growth essentially equals leaf death, separated in time by a certain linear quantity of living leaves, in the above instances: two leaves. The maximum carrying capacity or biomass for shoots in the SF population is equivalent to one mature leaf for the life of the shoot. The number of leaves sustained by shoots of *J. roemerianus* varies between different populations and has an inherent physiological basis (Watson 1952). An annual steady-state pattern of stability and equilibrium or homeostasis operates in each population of *J. roemerianus* and compares favorably with that reported by Williams and Murdoch (1972).

Since seasonal effects on leaf growth are minimal (Eleuterius 1974, 1976b), and because successive cohorts of new shoots are being produced in each population throughout the year, the average growth rate calculated for the cohort of shoots studied here during the periods of maximum growth is also the maximum sustainable growth rate. The period of active shoot growth is equivalent to maximum sustainable growth rate. The average rate of shoot growth is much less than the sustainable growth rate because the senescent leaf phase may be 2 to 4 times as long as the phase of active growth. The average rate of shoot growth calculated from total leaf length produced over shoot longevity showed a different rate than when calculated on the growth phase alone. For instance, at BFB the annual rate would be 0.5 cm/day, and at GB and SF the annual rates would be 0.3 cm and 0.1 cm/day, respectively. We feel that the maximum sustainable rates shown in Table 2 are accurate and more meaningful than annual rates shown above, especially in relationship to shoot growth and senescent patterns. Sustainable and average growth rates are obviously essential to an estimation of annual rates of growth.

Reliable estimates (E) of shoot age can be calculated from the number of leaves present on a shoot (N), the average plastochron (P), and average leaf longevity (L) for each population studied using the equation: $P(N - 1) + L = E$. For example: the age of a shoot that produced four mature leaves in the GB population would be approximately 38 months old, where $P = 8$, $N = 4$, $L = 14$. Similar estimates can be derived for shoots in the populations at BFB and SF. Comparison of estimates of shoot age with the actual age of a randomly selected group of tagged shoots from each population indicated that our method is reliable for any shoot within 1 or 2 months. Considering the wide variation in some populations of *J. roemerianus,* the method is very precise, has high usefulness, and represents a significant contribution to the biology of the rush.

The pattern of shoot production in *Spartina alterniflora* and *Scirpus olneyi* on the mainland coast of Mississippi

greatly contrasts with that of *J. roemerianus*. Generally all shoots within separate populations of the tidal marsh grass *Spartina alterniflora*, and sedge *Scirpus olneyi* arise simultaneously in the spring from the marsh surface in a synchronized manner in Mississippi. There are exceptions to this general pattern during years of mild winters. However, regardless of seasonality, all shoots within populations of *Spartina alterniflora* and *Scirpus olneyi* are about the same age. Consequently, all shoots reach maturity, produce flowers, and die at relatively consistent and predictable times within one year. This process, applicable to the Mississippi coast, may appear to contrast with reports on *Spartina alterniflora* by Hopkinson et al. (1978) for Louisiana, and Stout (1978) for Alabama. However, we feel that temperature differences related to latitudinal distances are responsible for these conflicting reports (Turner 1976). The lower part of Bayou La Fourche and Barataria Bay are located in the Mississippi River delta, a latitudinal distance of approximately 50 miles south of the Mississippi mainland coast. Stout (1978) worked in the marshes of Dauphin Island, a latitudinal distance of some 8 to 12 miles farther south than the mainland coast of Mississippi. However, Hopkinson et al. (1978) stated that *Spartina cynosuroides* and *Sagittaria lancifolia* have uniform developmental patterns represented by a single flush of growth. The point of our comparison here is to show that shoots of *J. roemerianus* are produced continuously, and mature and die in all seasons, whereas several other tidal marsh species have a single annual flush of growth. Thus, populations of the rush are composed of an array of shoots differing vastly in age. These wide ranges of shoot growth stages are described best and illustrated as a series of greatly overlapping harmonic curves. Changes in the vegetational structure of the rush stand cannot always be detected easily by direct observation or by sampling techniques like the Harvest Method. Each population of *J. roemerianus* is homogeneous as to vegetational structure, new shoots being initiated throughout the year while other, older shoots are dying. Therefore, only a small component or percentage of shoots composing the population die each year and these deaths span the entire year with a peak reached during late summer. Stout (1978) showed growth occurring throughout the year for *J. roemerianus* in Alabama.

Although seasonal conditions appear to affect individual shoots only moderately in our locale, these effects are generally not noticeable to the casual observer because all growth is suppressed equally on all shoots and the wide array of shoot growth stages obscures this process.

Furthermore, in some populations, e.g., SF, two entire crops of shoots may turn over every 22 months while in others a complete vegetational turnover may occur every 4 years. Alone, the total significance of this information would not be apparent. However, from preliminary studies on the same three populations of *J. roemerianus*, we learned that the recruitment of new crops of shoots or cohorts may

be six times greater in the SF population in comparison to that at BFB. Recruitment at SF appeared to be three times greater than at GB. This preliminary knowledge, combined with that of the present study, suggests an important pattern of growth. The SF population which seemingly would be a population of low productivity, based on standing crop estimates, may be one of very high net productivity, based on the large number of shoots per unit area of marsh and the rapidity of turnover. Although we are unable to develop fully these modes of production here because of incomplete recruitment and biomass data, it is important to mention that the net productivity of the very short leaved SF population may equal or exceed the net productivity in the very long leaved BFB population over the same period of time. We surmise that this phenomenon would not have been revealed by assessing standing crop from clip quadrats because the replacement shoots were obscured by dead shoots and the precision of the Harvest Method cannot measure these changes.

Our results agreed only in a general way with those of Stout (1978), Hopkinson et al. (1978), and Williams and Murdoch (1972), because our overall objective was different in that productivity as annual biomass or standing crop was not investigated. Stout (1978) used a combination of leaf counts and linear leaf measurements from random quadrats and related biomass for above ground to below ground determinations. Hopkinson et al. (1978) used standing crop from quadrats, and Williams and Murdoch (1972) used linear measurements of tagged leaves and standing crop making it more comparable to the present paper than the others. We disagree in the finer details of the growth kinetics reported by Williams and Murdoch (1972) in that there is no interval between the cessation of growth and onset of death, at least in the *J. roemerianus* of Mississippi. None of these papers showed clear patterns of shoot growth, longevity, senescence, and death. Furthermore, we feel that the compartments used in the production model of Williams and Murdoch (1972) were too broad: live leaves = all green, dying leaves (dead and green), and all dead. We have never seen mature leaves of *J. roemerianus* in Mississippi or elsewhere that were entirely green. Hopkinson, et al. (1978) stated that the *J. roemerianus* marsh they studied was in "transition" or changing vegetatively. They concluded their work by pointing out the difficulty of measuring "true net production" by the Harvest Method and the need for refinement in productivity techniques. Our paper presents techniques basic to improving future productivity work. Our method is much simpler, less time consuming, and more accurate than those previously used. Additionally, linear growth measurements, coupled with shoot demography and standing crop, may allow considerable clarification and insight into population structure, growth kinetics, and production of *J. roemerianus* tidal marshes.

In conclusion we emphasize that growth kinetics and longevity peculiar to *J. roemerianus* are vastly different between populations, and that high net productivity may be common to all populations of this tidal rush, although accomplished in different ways.

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